Can we measure brain efficiency? An empirical test with common marmosets (Callithrix jacchus)

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Can we measure brain efficiency? An empirical test with common marmosets (*Callithrix jacchus*)

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Illustrations: 2 Tables and 5 Figures

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Abstract

Various measures of brain size correlate with cognitive performance; however, the fit is not perfect, which bears the question whether brains also vary in efficiency. Such variation could be expected if a species faces constraints on brain enlargement, for example due to the impossibility of slowing down life-history as a consequence of predator pressure, while simultaneously experiencing selective benefits from enhanced cognitive ability related to particular ecological or social conditions. Arguably, this applies to Callitrichid monkeys and would lead to the prediction that their relatively small brains are particularly efficient in comparison to their sister taxa Cebus. This study investigated whether Callitrichids cognitive performance is *better than would be expected given their brain size* rather than comparing absolute performance between the taxa. As a measure of cognitive performance, we used the Reversal Learning paradigm, which is reliably and closely associated with brain size across primate taxa, and assessed performance in this paradigm (Transfer Index) in 14 common marmosets (*Callithrix jacchus*) as representatives of the Callitrichids. These marmosets were found to show higher performance than would be expected for their brain size, and this relative performance was also higher than the relative performance in capuchin monkeys. We outline how these effects may be due to the cooperative breeding system of the Callitrichids, particularly enhancement of behavioural and cognitive propensities associated with shared care and provisioning.

Key words:

Brain size, brain efficiency, common marmosets, cooperative breeding, inhibitory control, life history, predation, Reversal Learning, Transfer Index.

1 Introduction

Variation in brain size among primates correlates positively with various measures of cognitive ability, e.g. tool-use and social learning [Reader and Laland, 2002], tactical deception [Byrne and Corp, 2004; Whiten and Byrne, 1988] or cognitive ability more generally [Deaner et al., 2007]. However, large brains not only provide cognitive benefits in terms of enhanced cognition, but also incur costs, mainly with regard to energy requirements and life history [Aiello and Wheeler, 1995; Harvey and Clutton-Brock, 1985]. Because brain tissue is metabolically very expensive, species need to find some way of paying this energetic cost in order to afford a larger brain [Isler and van Schaik, 2006], as for example through tradeoffs in metabolism, increasing their total energy turnover or additional energetic inputs to the developing brains by cooperative breeding [Isler and van Schaik, 2009; Navarrete et al., 2011].

Additionally, brain enlargement has concomitant effects on life-history: bigger brains slow down development, which has to be compensated for by longer reproductive adult life span [Harvey and Clutton-Brock, 1985; Isler and van Schaik, 2009; Ross, 2004]. However, not all species can afford a slow life-history: Small body size makes disproportionately vulnerable to predation [Cheney and Wrangham, 1987; Isbell, 1994] and highly unpredictable survival due to high predator pressure favors fast life histories [Janson, 2003]. Consequently, a main constraint on brain enlargement is small body size and its associated fast life-history [Barrickman, 2008]: small bodied species facing high predator pressures simply cannot afford to evolve bigger brains despite the potential benefits of cognitive enhancement.

One possible way to compensate for this constraint may be to evolve particularly efficient brains, i.e. brains that provide higher levels of cognitive performance per volume unit.

However, this does not mean that we should expect all brains to perform at the same maximum level of efficiency; instead, every brain is as efficient as it needs to and can be, given phylogenetic constraint, physiological and behavioural strategies adopted by particular lineages, current adaptive pressures, and ontogeny. These ultimate factors result in trade-offs that lead to optimization of certain traits at the cost of others [Aiello and Wheeler, 1995 Isler, 2009]. Because the conditions that determine what needs to be present for survival differ from species to species, it should come as no surprise that efficiency may differ between them as does metabolism [Glazier, 2005] or vision[Jacobs, 2008; 2009].

Approaches that correlate brain size with measures of cognitive ability acknowledge that there is also always a proportion of variation that remains unexplained [Schoenemann, 2006]. This is because brains not only differ in size, but also with respect to other factors such as, connectivity, receptor density, or organization [Barton and Harvey, 2000; Herculano-Houzel et al., 2007b; Schoenemann, 2005]. Variation in such factors likely results in differences in brain efficiency. This alternative should be pursued whenever a species strongly relies on cognitive survival skills but at the same time faces serious constraints on further brain enlargement.

Within mammals, primates in general show an evolutionary history of brain enlargement [Boyd, 2006; Jerison, 1973; Martin, 1990] and commonly show larger brain sizes than equally sized mammals of other orders [Finlay et al., 2001; Martin, 1990]. This suggests that primates have opted for cognitive survival strategies, compared, for an extreme example, with low energy expenditure strategies such as found in species of the order Pilosa (sloths and their relatives)[MCNab, 1978; Nagy and Montgomery, 1980]. Primates therefore are a

particularly suitable order for investigating questions on brain efficiency as they rely particularly on cognitive performance for survival. To date no studies have addressed to what extent smaller bodied primates may compensate for this disadvantage by opting for at least some increase in brain efficiency. However, this would arguably be the most likely situation in which to find evidence for increases in efficiency.

Among primates, Callitrichids are the smallest bodied lineage with the shortest life-history [compare: Goldizen, 1987; Robinson and Janson, 1987]. They face high predation risk as evidenced both by attack rates and high levels of predator-related vigilance as well as avoidance behaviour [e.g: Goldizen, 1987]. In contrast, their sister taxa, the Cebidae, comprising the capuchin and the squirrel monkeys, have 7 – 13 times bigger bodies, and a 3 to 4 times longer life expectancy [Rowe, 1996], indicative of a lower extrinsic, predator related mortality, particularly in the capuchin monkeys . Callitrichid monkeys therefore fit the case of a primate genus unable to afford brain size enlargement, and thus one in which we may find evidence of increases in efficiency.

In the simplest case and in the absence of variation in efficiency, an inability to afford brain size enlargement would mean that a species is less cognitively complex than a similar, larger brained species. However, that this likely is not the case in Callitrichids is shown by a recent meta analysis that revealed that Callitrichids systematically outperform their sister taxa, the larger brained Cebidae, in all cognitive tasks in the social-cognitive domain [Burkart and van Schaik, 2010]. In non-social cognitive tasks, they performed at similar levels or lower. However, the direct comparison of Callitrichids vs. Cebines is highly conservative because Cebines have brains that are 4 to 6 times larger [Herculano-Houzel et al., 2007a; Stephan et al.,

1981] and absolute brain size is positively correlated with non-social cognition in primates [Deaner et al., 2007]. Therefore, similar or superior performance in Cebines compared to Callitrichids tells us little, as yet, about possible increases in brain efficiency. The question rather is whether Callitrichids perform better than would be expected for their brain size, compared to their sister taxa, in particular the much bigger bodied and longer lived capuchin monkeys.

Here, we propose to assess brain efficiency by (i) identifying a non-social cognitive measure that is closely correlated with brain size across primates and (ii) estimating brain efficiency by calibrating individual cognitive performance in this task by that predicted for the species based on brain size.

A good starting point for identifying a non-social cognitive measure closely correlated with brain size is the meta-analysis by Johnson, Deaner and van Schaik [2002] . They identified a global cognition factor "g", derived from a Bayesian meta-analysis of 27 primate species and across 9 non-social cognitive paradigms. "g" correlates well with various brain size measures, with overall brain size providing the best fit [Deaner et al., 2007]. In the present study, using Johnson's "g" for the direct comparisons of taxa, is not possible because it is a statistically derived index and thus not empirically measurable. Estimating brain efficiency requires comparing individual performance with that predicted based on the brain size of the taxon; an empirical paradigm is therefore indispensable. Firstly, we therefore aim at determining which single empirical approach, within those cognitive domains included in the meta-analysis, most closely estimates the theoretical global measure. Secondly, we aim at finding an empirical

methodology within that approach that was similarly tested in multiple primate species, particularly those of interest for this study.

A reanalysis of the data used by Deaner et al. (2007) indicates that of the cognitive paradigms included, Reversal Learning provides the closest fit with the global cognition factor (see details in methods section below). Reversal Learning is a pattern-discrimination paradigm whose key element is a reversal of reward contingencies. It thus measures cognitive flexibility in terms of the ability of the subject **to let go of a previously learned discrimination and shift to an alternative solution**. This finding fits well with the recent consensus that general cognitive performance, at least in the non-social domain, has much to do with flexibility and the ability to let go of old solutions and find new ones [Byrne, 1995; Gibson, 2001; Lefebvre et al., 2004; Roth and Dicke, 2005]. According to Roth & Dicke [2005] such flexibility forms a general ability underlying performance in a broad array of tasks. Thus Reversal Learning performance likely provides a good estimate of general cognitive performance. However, the reanalysis of the Deaner et al. (2007) data, while theoretically well supported, was based on an analysis of the studies themselves used for generating "g". It is thus circular and independent confirmation is needed, by demonstrating the relationship between "g" and Reversal Learning studies not included in the original meta-analysis.

Of the many Reversal Learning measures available, *Transfer Index* (TI) [Rumbaugh, 1997] has the advantage of controlling for various sources of variation common to other measures that make direct comparison of data difficult. In particular, TI reliably controls for the level of learning achieved prior to reversal, bringing all subjects to an equal performance level before testing them on the cue reversal [Rumbaugh, 1997; 1971], an essential element

allowing for more accurate comparisons across studies. Additionally, the Transfer Index methodology has been described in great detail [Rumbaugh, 1997] so that replicability is assured and data from different labs may confidently be compared. Furthermore, reliable Transfer Index data are available for numerous primate species including multiple Capuchin individuals [Beran et al., 2008; Delillo and Visalberghi, 1994]. However, to our knowledge, none using a comparable methodology has been reported for any member of the Callitrichid family to date.

Thus, the aim of the present study is to place brain efficiency of common marmosets (*Callithrix jacchus*) in relation to that of their sister taxa with the lowest predation pressure, the capuchin monkeys [using data from Beran, M. pers. com. and Delillo and Visalberghi, 1994]. We predict that even though in absolute terms, the capuchin monkeys may well outperform the marmosets; the latter may show higher performance relative to their brain size. In order to do so, we first confirm that Reversal Learning and specifically the Transfer Index methodology is a reliable and good empirical estimator of non-social cognitive ability in nonhuman primates. We then measure Transfer Indices in a large sample of common marmosets (*Callithrix jacchus*) as representatives of the Callitrichids, and compare their absolute and relative performance to their sister taxon.

2. Materials and Methods

2.1 Does Reversal Learning and Transfer Index in particular, reliably estimate general cognitive ability "g"?

2.1.1 Transfer Index

168 The Transfer Index is a measure used to quantify performance in Reversal Learning
169 paradigms. It is measured in terms of the number of correct choices in a pattern discrimination
170 task relative to a set number of conducted trials [Beran et al., 2008; Delillo and Visalberghi,
171 1994; Rumbaugh, 1997]. On achieving the pre-determined learning level in an initial
172 discrimination task, the rewarded contingencies are reversed and performance under these
173 conditions is measured over a set number of trials. Commonly, Transfer Index is calculated by
174 placing the reversal performance relative either to a low (67%) or a high (84%) initial
175 association level.

176 The somewhat arbitrary choice of percentage is the result of the original testing
177 methodology [Rumbaugh, 1971] which for reasons of comparability was maintained in
178 subsequent studies. The former corresponds to performance slightly above chance and reflects
179 a very weak association formation between reward and pattern, with the subsequent reversal
180 of reward contingencies likely requiring little more than weak extinction. The latter reflects a
181 strong association requiring more active inhibition of the pre-potent response in order to
182 obtain the reward in the reversal situation. It is thus possible that the two different pre-
183 reversal criteria tap into different cognitive processes rather than reflecting different ends of
184 the same process. The TI index is calculated as follows for both high and low levels of pre-
185 Reversal Learning [Beran et al., 2008; Delillo and Visalberghi, 1994; Rumbaugh, 1997]:

186 **Transfer Index = reversal performance (%) / pre-reversal performance (%)**

187

188 **2.1.2 Comparative analyses**

In order to independently confirm whether the Reversal Learning paradigm predicts "g" reliably, we searched the literature for studies on Reversal Learning tasks generally and Transfer Index specifically. We searched the databases "ISI Web of Knowledge", "PubMed", "PrimateLit" and "PsycINFO"; Reversal Learning studies included in the Deaner meta-analysis were excluded. Wherever invasive methods or other experimental manipulations where used, we only collected the data for the control group. For Reversal Learning, data for each primate taxa in each study were converted into "mean percent correct" (mean trials (100%) and mean errors (100% - percent correct) as studies used and reported different total numbers of runs and errors. Studies for which this was not possible were excluded due to lack of comparability. The Reversal Learning measure and Transfer Index values were compared separately to "g" to avoid circularity. Reversal Learning studies were limited to the primate genera for which Transfer Index data were available to increase comparability.

12 primate species were found in which Transfer Index has been measured: *Gorilla, Pongo, Pan* (without the bonobos), *Hylobates, Cercopithecus, Miopithecus*, *Lemur* and *Microcebus* [See Rumbaugh and Gill, 1973; Wilkerson and Rumbaugh, 1978] *Macaca* [Washburn and Rumbaugh, 1991*] Cebus*, *Saimiri* [Beran et al., 2008; Delillo and Visalberghi, 1994; Rumbaugh and Gill, 1973] and *Callithrix* (Strasser et al, this study). For all species, Transfer Index values for both high and low levels of association formation prior to reversal were available.

Additionally, we found 24 publications on Reversal Learning for these primate genera for which it was possible to extract a value for "mean percent correct". Unfortunately, many publications reported their data in such a way that it was not possible to convert it into a

percentage. These publications had to be excluded as they were not in any way comparable. A total of 40 measures emerged from these twenty-four articles, (sometimes more than one experiment was conducted for a certain study or more than one of our primate genera was subject in the study) which were collapsed into one weighted average value per genus (Table 1, appendix).

2.2 Transfer Index in common marmosets

2.2.1 Subjects and Maintenance

A total of 14 adult common marmosets in four family groups housed at the Primate Station of the University of Zurich were tested, ranging in age from two to six years. The groups lived in standardized cages (2x2x1m) containing a sleeping box, a water dispenser, an infra red lamp (150W), a rack to hold food bowls and a standard branch arrangement. The floor of the cages was filled with a layer of mulch that was turned and wetted weekly. The light regime consisted of daylight, and additional electric light from 8 a.m to 6 p.m. and UV light (300W) from noon to 12:30 p.m. Animals had free access to an outdoor run on a daily basis from April to October. This access was inhibited during the testing sessions. Husbandry regimes for all animals were identical. A morning meal of mealworms, gum and porridge was followed shortly before noon by a main meal of chopped fruit/vegetables and, on non-test days, by a small treat consisting of egg or a nut at 1 p.m. Water and monkey chow were provided ad-libitum. On test days mealworms and the treat were provided after the test, generally towards 4 p.m. Thus, animals used in the tests were not food deprived which also reduced hunger induced motivational differences between individuals.

All tests were conducted in a separate testing room in which the test cage was located. Animals entered this testing enclosure via a PVC tube which ran into the adjacent room containing the home cages. Animals voluntarily entered these tubes and the testing room and were not directly handled. Individuals were familiar with the testing room and enclosure, having been given the opportunity to explore and play there freely. During testing the pair or group of animals was called into the waiting enclosure of the test cage, visually isolated from the actual testing area, and individually allowed over for the actual test procedure. The original research reported in this study was performed under guidelines established by the National Veterinary office of Switzerland and licensed to be performed by the Veterinary office of the Canton of Zurich.

2.2.2. Apparatus and Procedure

Animals were initially habituated to a wooden presentation board containing two food wells, and to the fact that rewards could be obtained from the wells (Apparatus with measurements, Figures 1 & 2, Appendix). Subsequently individuals were shaped to move a square of wood to reveal the baited well. Finally the baiting was hidden from the individual by placing a large visual barrier between the animal and the presentation board; only one of the two wells was randomly baited, but both wells covered by a square of wood.

For the actual test, ten pairs of visual discrimination patterns were used, consisting of black on white or white on black geometric figures (pattern pairs and sequence used, Figure 3, Appendix). Each animal received the same sequence of pairs of patterns and in each pair the same randomly chosen pattern was termed the initially rewarded discriminand (S+). Black and

white patterns only were used to avoid bias, as it has been shown that Callitrichid individuals may have either a dichromatic or trichromatic visual system. Thus different colours may be easier for certain individuals to see and discriminate [E.g: Hunt et al., 1993; Jacobs, 2007].

Individuals were tested a maximum of one session per day, consisting of a total of 11 trials in which they were able to pick one of the two covered wells. The choice of 11 trials was made to ensure high levels of motivation and because this corresponds to the number of trials suggested and used by Rumbaugh [1971] as well as in the studies by Delillo & Visalberghi [1994] and Beran et al [2008]. A trial consisted of the pulling back of the presentation board, the placement of the upright visual barrier to hide baiting, the baiting of the pseudo-randomly determined well and re-covering of the wells with the patterned squares of wood. This took up circa 15-20 seconds of time. If successful, animals were given time to consume the reward. If they were incorrect the next trial was started. If an animal refused to choose, the trial was recorded as a refusal after one minute and the next trial begun. If an animal refused to choose three times in a row in a given session, the testing was terminated for that day. Termination occurred in less than 5% of trials.

Identical covering of the wells was ensured by always employing the following procedure: Squares were placed, two-handed, over the widest part of the well such that an equal excess of the square extended right and left of the well (visual fit, in the region of 2mm on either side), then the square was moved forward, again two-handed, to fit tight with the front of the presentation board. Patterns were printed on paper, with overlap, so that they could be attached to the underside of the squares with tape. Thus only the pattern was visible to the animal and not any part of the tape.

In the early problems (pattern pairs 1-3), animals were aided during the acquisition of the discrimination in that if they failed to choose the correct pattern for four consecutive trials, the individual was also allowed to uncover the second well during the same trial. The choice, however, was recorded as incorrect. The position of the S+ was pseudo-randomized (not more than three consecutive trials in the same location) using computer generated random number lists. As TI performance has been shown to be unrelated to the speed of the initial acquisition but rather to how strongly the discrimination is learned [Rumbaugh, 1997] the aiding explained above is unlikely to have any effect on TI performance as it affects primarily the speed of acquisition, degree of learning being controlled for in any case. Indeed, aiding had no influence on the performance of the marmosets in this study (see results section).

To avoid cueing of the individual, the experimenter pushed the presentation board within reach of the animal with bimanual, symmetrical movements and placed her hands by her side afterwards, avoiding direct eye contact with the subject and either of the covered wells.

Once a criterion of at least seven correct out of 11 was achieved, corresponding to the lowest learning criterion suggested by Rumbaugh [1971], the reversal session was conducted on the same or the next day. The decision was made based on the motivation shown by the animal. Motivation was taken into consideration because there is increasing evidence that lack of motivation can lead to reduced performance producing a falsely low indication of the individual's cognitive capabilities (Addessi, E. pers.com.). Thus, if the individual after reaching criterion still showed great interest, indicated by alert sitting at the front of the enclosure, focused attention on the board, the patterns or the experimenter the reversal was conducted.

However, if the animal showed indications of sinking motivation, indicated by increasing bouts of inattention or moving away from the testing board toward the exit, testing was conducted the next day. In these latter cases, prior to the reversal, individuals were tested on the original discrimination in three 'reminder' trials during the test day. These three trials were included in the calculation of pre-reversal performance. This did not have any significant effect on performance (see result sections).

In the reversal phase, 11 trials with the reversed reward contingency were run. The first served to signal the reversal of contingencies and only performance on the subsequent ten was used to calculate the Transfer Index. No help was given to subjects during any reversal trials or any of the 3 reminder trials. In sum, the test procedure was identical to that of Rumbaugh [1971] including the use of 11 trials as the basic "unit" with which to measure pre-reversal performance and the use of 64% (7 correct out of the 11) as the lowest learning level for which reversal was conducted.

2.2.3 Data coding and analysis

Each session was videotaped and the choice (correct/incorrect) by the individual for each trial noted. The trial notes were double-checked using the video footage in which choices were straight forward to determine, requiring the animal to move to the left side of the enclosure, or the right. There were no ambiguous cases. Transfer Index for each individual and for each problem was determined across the 10 problems. TI(Low) was calculated based on performance on problems in which pre-reversal performance was 7 or 8 correct out of the 11, and TI(High) based on a pre-reversal performance of at least 9 correct out of 11.

Analyses were conducted using SPSS 16.0 and JMP 7.0. Continuous data were tested for normality (Kolmogorov-Smirnoff) and equality of variances (Levene) and where possible parametric statistics were applied.

2.3 Capuchin monkeys

For the capuchin monkeys, we used the data from Delillo [1994] and Beran [2008 and pers.com]. The experimental design for the common marmosets was modelled as closely as possible after these studies. Thus, with the exceptions below, the methods for both species were identical. The main difference was that the marmosets discriminated between pairs of black and white patterns rather than between colourful, three-dimensional objects. For the capuchins the objects were baited with peanuts, candy or sunflower seed, depending on the preference of each subject. A choice was scored when the individual manually selected and moved one of the objects (in capuchins) or one of the patterned squares (marmosets).

The Beran data consisted of a large number of discrimination problems (over 50 in all cases) conducted for each of the individuals, and in some cases the reversal was conducted at lower levels of learning than the commonly used 67%. To assure comparability, we used performance in the first ten discrimination problems in which at least 67% pre-reversal performance was reached.

2.4 Comparing brain efficiency:

Brain efficiency was assessed by correcting effective task performance of each individual by the species value for this task, as predicted by a comparative analysis across all

primate genera for which TI data is available. The analyses were based on TI(High) which turned out to explain the largest proportion of variation in "g" (see results section). In a first step, the predicted Transfer Index value for both marmosets and capuchins was generated via a comparative analysis of the Transfer Index against brain size across the 12 primate genera. This produced a regression line reflecting the predicted values for each species in this task based on their brain size (see Figure 4). The Transfer Index data for the 12 genera used to generate the predicted values came from the sources cited in the section above.

Absolute brain size (endocranial volumes) were taken from Isler et al. [2008]. To control for phylogenetic relationships, independent contrasts were calculated using Mesquite [Maddison and Maddison, 2007] using the phylogeny from Bininda-Edmonds et al. [2007]. Predicted Transfer Index values were computed both including and excluding the value for Common marmoset from the present study (see results section). Excluding this value from the comparative analysis provides a more empirically rigorous test, while including it is statistically more exact.

In a second step, the effective deviation of marmoset and Capuchin individuals mean TI (High) task performance from the species predicted performance value was calculated by subtracting the latter from the former. In effect, the residuals of individual performance from the species mean were computed. **Thus, efficiency was estimated as the degree to which individuals average performance across 10 tasks deviated from the expected performance in this task based on brain size measures alone.** A t-test was then performed on the data, comparing the efficiency values for the Callithrix individuals with those of the Capuchins. All tests are two-tailed.

3. Results

3.1 Does Reversal Learning, and Transfer Index in particular, reliably estimate general cognitive ability "g"?

Both Reversal Learning (r^2=-.604*, p=0.037) and Transfer Index were correlated with "g", but Transfer Index explained more of the variance in "g". Transfer Index based on a high level of initial acquisition, arguably requiring more complex inhibitory processes, was more strongly associated with "g" (TI (high): r^2=-.850, p<0.000; TI (low): r^2=-.750, p=0.005). Explaining a third more of the variation in "g", TI (high) appears to more accurately measure general cognitive ability.

Not only do Reversal Learning Paradigms show a very good fit, but using a highly controlled methodology such as Transfer Index results in an enormous increase in predictive value. This confirms the finding of Deaner (unpublished) and also shows that using a clearly defined methodology removes much random error.

3.2 Transfer Index in common marmosets and capuchin monkeys

On average the marmosets required 28 trials to reach criterion and there was no correlation between the trials required for reaching the pre-reversal criterion and reversal performance (with TI: Rho= -0.3, p=0.738; with percent correct reversal: Rho= 0.001, p=0.991). This sample of common marmosets showed a TI (Low) of 0.695 and a TI (High) of 0.582. Pre-reversal criterion had a significant negative effect on Transfer Index when controlling for potential effects of individual as a random factor and reversal problem as a covariate (F = 9.337; p = 0.003, dF:1).

Neither individual (F = 0.313, p = 0.976, dF: 13) nor cumulative problem number (representative of a learning to learn effect) (F = 0.060, p = 0.808, dF: 1) had a significant effect. Over the ten problems, there was no significant difference in Transfer Index (Low and High) between the sexes (Low: t=0.340, df = 13 p=0.740; High: t = 0.834, df = 13 p= 0.421, N=14), breeding status (Low: t= -0.214, p= 0.831, df = 13; High: t = -0.182, p= 0.859, df = 13 N=14), and there was no correlation with age (Low: Pearson R^2= -0.134, p= 0.678; High: R^2 = -0.203, p= 0.601, N=14).

In Capuchins, a clear effect of pre-reversal criterion was also found (F=6.821; p=0.011, dF = 1), with animals performing more poorly in reversals of previously more strongly learned pattern discriminations. In contrast to common marmosets, capuchins show a clear effect of individual (F=11.585; p<0.000, dF = 1) as well as a learning to learn effect (F=18.185; p<0.000, dF = 1), with animals performing better on reversals carried out in later problems. The sample for the analysis above was limited to data from only the 5 individuals from the Beran dataset because no sufficiently detailed data are available for the 4 subjects from the De Lillo Capuchin dataset. The limited capuchin dataset (N=5) precludes a meaningful analysis of sex and age differences.

In the marmosets, conducting the reversal on the same or the next day produced no significant differences in reversal performance when controlling for pre-reversal criterion as a covariate and individual as a random factor (the latter included to control for pseudo-replication effects) (F = 0.573; p = 0.871, dF: 13).

Reversal performance at the lowest level of pre-Reversal Learning was significantly higher than that at higher levels when controlling for individual differences (F = 4.517, p= 0.036, dF=1).

Additionally, performance between the lowest level of learning and higher levels were not correlated (marmosets: Pearson = -0.181, p= 0.535, N=14; capuchins: P=0.214; p=0.584, N=9). An overview of each marmoset subject's performance in every single discrimination, including the criterion achieved, reversal performance and trials to criterion is listed in Table 2 of the Appendix.

3.3 Comparing brain efficiency

Figure 4 shows the correlation between Transfer Index (TI (HIGH) and brain size (endocranial volume, converted to the natural logarithm (LnECV). Species predicted values are represented by the regression line. The regression has been calculated including (Figure 1) and excluding the marmosets (values for both are listed in Line 413). For both, independent contrasts were computed (IC including marmosets: p= 0.0387; excluding: p=0.0521).

Figure 4: Least-squares regression of Transfer Index (high criterion) vs. Ln brain size across primates (N= 12 primate species, R2=0.594, p=0.001) common marmosets (star) exhibit a relatively higher Transfer Index for their brain size than capuchins (large dot).

Species predicted values indicate the TI(high) that would be expected for a species based on their brain size, and are as follows:

For capuchins: 0.56 (regression including common marmosets);

0.55 (excluding common marmosets)

For marmosets: 0.39 (regression including common marmosets);

0.37 (excluding common marmosets)

To identify whether the Transfer Index (High) of common marmosets deviates more strongly from the species predicted value compared to that of the capuchin monkeys, we compared Transfer Index (High) value residuals of individuals of both common marmosets (n=11) and tufted capuchins (n=9). The results show that common marmoset individuals have a significantly higher residual from the value predicted for their brain size than do tufted capuchin individuals (t= - 2.447, p=0.026, Figure 2). This holds even in the more statistically conservative, but less empirically rigorous, case of using predicted values based on a regression including marmosets (t=-2.268, p=0.037).

Figure 5: Boxplot of the difference between observed and predicted Transfer Indices (High criterio) for common marmosets (N=14 individuals) and tufted capuchins (N=9). The two species differ significantly (Student's t-test, t= - 2.447, p=0.026). The Boxplot shows the median value, interquartile range and the tenth percentiles for each species.

4. Discussion

The aim of this study was to assess whether adaptive pressure on brain efficiency can be expected where a species faces a constraint on further brain enlargement despite clear benefits accruing from high cognitive performance. Callitrichid monkeys arguably face strong

454 constraints on brain size increases due to high predation risk and the concomitant effects of
455 life-history on brain size.

456 Based on the finding of surprisingly high cognitive performance of Callitrichids
457 compared to Cebines in the social domain, our prediction was that common marmosets, faced
458 with large constraints on brain size increase, show enhanced brain efficiency, and cognitive
459 performance above what would be expected based on brain size alone. We found that this was
460 indeed the case, common marmosets perform significantly better than predicted for their
461 brain size compared to their larger sister taxa the capuchins.

462 In order to reliably show this, we firstly provided independent confirmation that the
463 Reversal Learning paradigm is a good empirical estimator of general cognitive ability. In
464 particular Transfer Index using a high level of initial association formation showed a
465 considerably closer fit with the global cognition measure than TI (Low) or Reversal Learning
466 more generally. This may provide support for the contention that the two different pre-
467 reversal criteria tap into different cognitive learning processes. Indeed, the fact that
468 performance at low levels of learning was not correlated with performance at higher levels in
469 both common marmosets and capuchins supports the idea that different cognitive processes
470 are involved. Arguably, the extinction of an association may be more relevant for reversing
471 weak associations such as formed during TI (Low), while active inhibitory processes may
472 emerge as strong associations are formed during TI (High). However, to date this remains
473 speculative but provides a good starting point for further research into this question.

474 The Transfer Index performance of common marmosets tends to be higher compared
475 to Reversal Learning studies in Callitrichids from earlier decades, even though methodological

differences preclude a direct comparison [reviewed in: Deaner et al., 2007]. However, our reassessment is consistent with results reported by Gaudio and Snowdon [2008] on cross-dimensional Reversal Learning in cotton-top tamarins (*Saguinus oedipus*), where individual performance was found to be surprisingly high. This, together with the results of the meta-analysis presented in Burkart & van Schaik [2010] is consistent with the idea that some enhancement of brain efficiency has taken place within this lineage.

Obviously, additional studies comparing relative cognitive performance including more callitrichid species and different cognitive paradigms are necessary to further confirm this conclusion. However, the question arises of how such an increase in brain efficiency may be explained? Particularly, questions arise about the nature of the benefits that enhanced cognitive performance provides for marmosets that would provide the selective pressure needed to enhance efficiency.

The increase in socio-cognitive performance found in the meta-analysis of Burkart and van Schaik can be attributed to the cooperative breeding system of the Callitrichids. Broadly defined, cooperative breeding refers to reproductive systems in which individuals other than parents help to care for and provision offspring [Garber and Leigh, 1997; Hrdy, 2009]. While Callitrichids show a strong degree of cooperative breeding, their sister taxa engage in significantly less allomaternal care [Fragaszy et al., 2004 ; Perry, 1999]. Shared care and provisioning is associated with behavioral propensities such as increased social tolerance, a tendency to pay attention to the whereabouts and behaviors of group members, and spontaneous prosociality, [reviewed in: Burkart and van Schaik, 2010]. These propensities can

497 explain their increased performance in many socio-cognitive tasks, but how performance in
498 non-social cognitive tasks may be affected is less straight-forward.

499 Obviously, cooperative breeding per se does not require advanced cognitive abilities
500 given its occurrence in very diverse lineages including primates and other mammals, birds, fish
501 and even insects [e.g.:Clutton-Brock, 2002]. However, the proximate regulation of helping
502 behavior is likely to vary between lineages, as a function of the kind of helping behavior
503 involved and the original cognitive organization that was present before a given lineage
504 adopted a cooperative breeding system. Among primates, a candidate proximate process that
505 might have been enhanced is inhibitory control, which is arguably required by Callitrichid care-
506 givers for the successful active provisioning of infants with high value foods that requires them
507 to inhibit their response to eat the food themselves as well as in many situations in which they
508 show high levels of social tolerance.

509 Inhibitory control has also been argued to be a major component of Reversal Learning
510 performance [Kralik, 2005; Kralik et al., 2002; Santos et al., 1999] and thus a component
511 measured by the Transfer Index task. While this premise appears reasonable, a direct
512 correlation between reversal learning and inhibitory control still needs to be shown. However,
513 if the better than expected performance of marmosets in Reversal Learning is due to better
514 inhibitory control, they should also perform better than expected for their size in inhibitory
515 control tasks (such as detour reaching [MacLean, 2011], delay tolerance [Addessi et al.; Amici
516 et al., 2008] or reversed reward contingency [Shifferman, 2009]).

517 A further aspect is that a trait complex such as allomaternal care and its associated
518 motivational and cognitive propensities is likely to be largely innate and rely less on individual

519 ontogenetic learning in small brained cooperative breeders such as Callitrichids because it is
520 evolutionarily so essential for the taxa. This would mean that specific essential abilities are
521 selectively enhanced and, being strongly canalized, shown in all individuals to a similar degree.
522 If cooperative breeding and its underlying propensities are indeed largely innate, less variation
523 between individuals and, in this particular case, the sexes and age classes is expected in any
524 associated measure. This is exactly what is found for the Transfer Index values in common
525 marmosets, in contrast to the capuchins where strong effects of the individual are found as
526 well as clear learning to learn effects, both indicative of more individual learning based
527 cognitive performance.

528 On current evidence, it is not possible to decide whether the observed increase of
529 efficiency in non-social contexts is a byproduct of cooperative breeding or due to selective
530 pressures acting on physical-cognitive domains directly, due to ecological reasons for example
531 [Stevens et al., 2005]. Future work will first have to provide further evidence for a relative
532 increase of performance in non-social contexts in Callitrichids. To further evaluate which of the
533 possibilities raised above might be responsible for such a pattern, additional data from other
534 primate species that differ in ecological conditions or breeding system, yet facing similar
535 constraints on brain size increase are indispensable.

536

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